



How orb-weavers find and grasp silk lines

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Abstract. Spiders are effectively blind with respect to the lines in their own webs. Species in four orb-weaving families solved the problem of finding lines by tapping with their anterior legs, like a blind man with his cane, and then “following” these anterior legs with more posterior legs, which grasp lines that the anterior legs are already holding. Following behavior occurs during several stages of orb construction, and probably economizes on searching time and effort. The movements of following legs are finely adjusted to the morphological details of the grasping structures on their tarsi (the middle claw and its associated serrate accessory setae): the small searching movements made by following legs have consistent orientations: legs I and II move prolaterally, while legs III and IV moved retrolaterally. These orientations are appropriate to bring the asymmetrically placed middle claw and accessory setae into contact with the line. Spiders solved the additional problem of grasping lines that are more or less parallel to the long axis of the leg by using a previously unrecognized movement; they rotate the distal portion of the leg on its longitudinal axis, orienting the middle claw so that it is more or less perpendicular to the line. As an orb-weaver moves across her web, she probably constantly adjusts the rotation of each leg to align its middle claw perpendicular to the lines that it grasps.

Keywords: Middle tarsal claw, accessory setae, leg movements, web construction behavior

An orb web spider confronts special problems in finding and grasping lines as it moves on its web, because orb-weavers are often active at night and are in any case effectively blind with respect to the lines under which they are walking. Their eyes are probably not capable of resolving such fine objects (Barth 2002), as well as oriented inappropriately, being directed dorsally and laterally, while the web lines are usually ventral to her body. The spider instead relies on her legs (usually legs I and II) to locate new lines. This paper concerns behavioral solutions to these problems.

An animal’s behavior always depends on its morphology, so a convenient place to begin is the tarsal morphology involved in grasping web lines. It was established long ago that modifications of the tarsal claws and the serrate accessory setae enable spiders with three tarsal claws to firmly grasp and then release single silk lines (Nielsen 1931; Wilson 1962; Foelix 1970, 2011). Observations with both a dissecting microscope (Nielsen 1931; Wilson 1962) and a scanning electron microscope (Foelix 2011) showed that the middle claw is lowered (as a unit with the lateral claws) to trap the line against the teeth on one (or perhaps more) of the stiff but nevertheless somewhat flexible serrate setae nearby (Fig. 1), where it is squeezed between the ventral surface of the claw and the deflected setae (I will call this “grasping” in the descriptions below). When the line is bent sharply between the serrated accessory setae and the middle claw, the spider’s grip is prevented from slipping. When the middle claw is lifted slightly, the grip on the silk is loosened, and the line can slide under the middle claw (Wilson 1962). When the claw is lifted completely, the grip on the line is released: the tension on the line itself, along with the straightening movements of the setae, are thought to propel the line away from the claw (Nielsen 1931). This interpretation of the functional association between the middle claw and the serrate accessory setae is supported by the correlation between their positions on the tarsus: on legs I and II the middle claw is directed prolaterally, and most of the setae are on the prolateral side of the tip of the

tarsus; on legs III and IV, the middle claw is directed retrolaterally, and most of the setae are on the retrolateral side of the tip of the tarsus (Nielsen 1931). These asymmetrical positions of the middle claw and the serrated accessory setae are correlated with the positions in which the spider often holds her legs; legs I and II are often directly anteriorly and legs III and IV are directed posteriorly (Nielsen 1931).

Additional evidence favoring this interpretation of a grasping function was obtained when the serrate accessory setae were experimentally removed from the tarsi of all of the legs of *Araneus diadematus* Clerck, 1757 (Araneidae); the spider experienced difficulties in both web construction and in climbing vertical lines (Foelix 1970). Spiders climbed a line five times more slowly after the serrated accessory setae had been removed (Foelix 1970). Comparative morphological data from other species also support this interpretation. A species which lacks the setal teeth, the amaurobiid *Amaurobius ferox* (Walckenaer, 1830) slipped while attempting to climb a vertical dragline (Nielsen 1931). *Hyptiotes paradoxus* (C.L. Koch, 1834) (Uloboridae) which builds a triangular web, holds a signal line to her web under substantial tension with her legs I for long periods while she waits for prey, both the middle claws and their serrated accessory setae are especially stout and have numerous teeth.

The present paper adds a behavioral dimension to this classic morphological story. The logic is based on the recognition that an orb web spider probably never sees the lines in her web during web construction. Web spiders are known to employ two techniques to find lines to grasp: tapping with their legs to contact lines (like a blind man with his cane) (Vollrath 1992), and “following”, in which one leg follows another to grasp a line that the other has already found and grasped (Hingston 1922; Eberhard 1972, 1987a). Following allows more posterior legs to economize on time and effort by following more anterior legs in both space and time. In simple terms, the spider locates and grasps a “new” line with a more anterior “leading” leg as she moves forward,

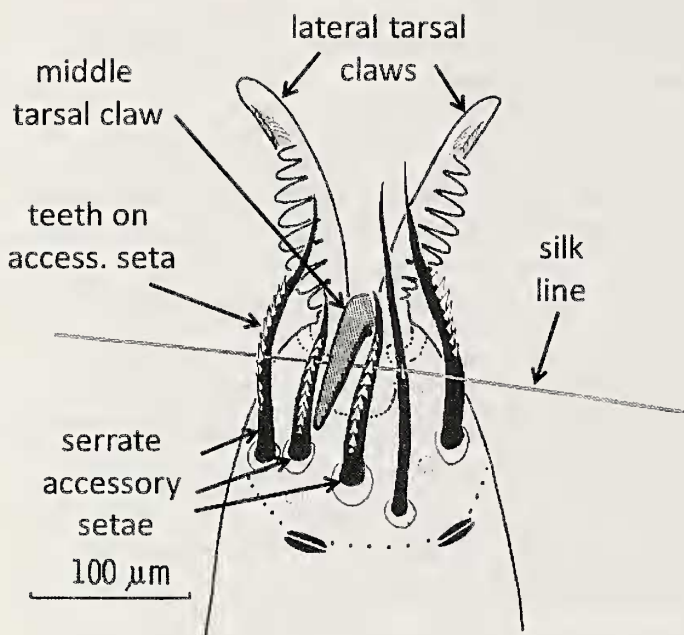


Figure 1.—A schematic representation of how the middle claw of *Araneus diadematus* grasps a line by pressing it against the teeth on nearby serrate accessory setae. The claw is grasping the line only loosely, as it does not cause the line to bend against the setae (from Foelix 2011).

and then moves her more posterior (nearly always the adjacent, ipsilateral) “following” leg forward and grasps this same line; soon afterward, the leading leg usually releases its grip and moves forward. Sometimes a line is passed to two or three more posterior legs in succession.

Following behavior was first described in the sticky spiral construction behavior of *Nephila pilipes* (= *maculata*) (Fabricius, 1793) (Nephilidae) by Hingston (1922), then much later by Eberhard (1972, 1987a) in hub construction behavior of *Uloborus diversus* Marx, 1898 (Uloboridae) and *Leucauge mariana* (Taczanowski, 1881) (Tetragnathidae), and in sticky spiral construction of at least eight genera of Araneidae, three of Tetragnathidae, and one of Nephilidae (Eberhard 1981). In these previous descriptions, all of which were based on observations with the naked eye, the following leg was said to step directly to grasp the line already being grasped by the leading leg. As will be shown below, video recordings have revealed that these descriptions were somewhat imprecise: the following leg usually executes a small “short distance” searching movement, usually lasting on the order of about 0.1s, just before the leg contacts the line and grasps it, rather than moving directly to it.

Short-distance searching movements are extremely predictable in time when a following leg nears the line being held by a leading leg. In addition, the identities and locations of the lines for which the spiders are searching are clear. This makes it possible to study short-distance searching behavior with unusual detail and confidence. There are, for instance, no complications regarding other possible functions of these movements such as locomotion or searches for other objects. It was thus possible to deduce the probable functions of the consistent orientations of legs during short distance searching in relation to tarsal morphology.

The second objective of this paper is to revisit an unresolved problem in understanding how spiders grasp lines. The classic description of grasping assumes that the line is more or less perpendicular to the longitudinal axis of the tarsus (Fig. 1); it does not explain how a line could be grasped when the line is oriented more or less parallel to the long axis of the spider's leg. As noted by Nielsen (1931), spiders nevertheless routinely grasp lines with these orientations. This paper describes observations that suggest how this is done.

METHODS

Video recordings of orb web construction were made with a 30 frames per second (fps) hand-held SONY HDR-SR11 camera equipped with a +2 close-up lens, either in captivity with *Zosis geniculata* (Olivier, 1789) (Uloboridae), *Cyclosa monteverdii* Levi, 1999 (Araneidae), and *Nephila clavipes* (Linnaeus, 1767) (Nephilidae), or in the field (the other species in Table 1). In most species only a single individual was filmed, but in all cases, the web being built was typical and the activity was repeated many times. Not all details were always clear at all times in the recordings, but all characterizations were based on >10 clear cases (see Table 1). Sticky spiral construction in vertical webs was usually filmed while the spider was above as well as below the hub; all descriptions of sticky spiral construction involved spiders in the outer portions of their orbs. Illumination for *Z. geniculata* was a near infra-red light (using the “night shot” feature of the camera); the others were illuminated by ambient light. In descriptions of the construction of spiral lines, the legs on the side farther from the hub are termed “outside” legs (e.g., leg oI), and those nearer the hub are termed “inside” legs (e.g., leg iI); in all cases, none of the lines that were grasped (radii, hub spiral, temporary spiral lines) were sticky.

One leg was characterized as following another if it consistently moved to and grasped a line near the point where that same line was already being held by the leading leg, and if the leading leg soon afterward released its hold on the line (typically it moved forward to find and grasp another line). “Short-distance searching” movements were small amplitude movements (on the order of one or a few diameters of a tarsus) that were executed by the tip of a following leg approximately 0.1s before it grasped the line being held by the leading leg; the movement of the following leg preceding short-distance searching was usually direct, presumably because the approximate location of the line was already known by the spider. Short-distance searching movements differed from the much larger-amplitude “long distance” searching leg movements that were often repeated several times in a row when the spider explored an empty space by waving or tapping with her legs. To improve the clarity of behavioral descriptions, I will employ the illusion (as in other languages such as German, French and Spanish) that all spiders are females; in point of fact, all behavioral observations involved mature females.

Recordings were analyzed frame by frame to determine the side of the leg (prolateral vs. retrolateral) on which a following leg first made contact with the line that it grasped. Particular attention was paid to the movements of following legs in the last frame or two before the leg grasped the line. The direction in which the line was displaced by the following leg in the first image in which contact occurred also gave especially clear

Table I.—A tentative list of possible uniformities in two details of leg movements, following and prolateral vs retrolateral short-distance searching movements, that were performed during orb construction by a serendipitous sample of species whose construction behavior I happened to have recorded (not all stages are represented for all species). All recordings were made in the field except those of *Cyclosa montevedii*, *Nephila clavipes*, and *Zosis geniculata*. In most species only a single individual was filmed, but in all cases the activity was repeated many times. Sticky spiral construction was characterized in the outer rather than the inner half of the web, and usually included behavior above as well as below the hub in vertical orbs. One leg was characterized as “following” another if it consistently moved to and grasped a line near to the point where that same line was already held by the other, leading leg, and if the leading leg then quickly released its hold on the line (typically moving forward to find and grasp another line). “Short-distance” searching movements were the generally small amplitude movements executed by the tip of the leg approximately 0.1s before it grasped a line; they were especially clear when one leg was following another (probably because the approximate location of the line was already known by the spider). Legs are indicated by “o” and “i” to indicate their positions during construction: “outer” legs were those directed away from the hub while the spider was spiraling around the web building hub, temporary and sticky spiral lines; “inner” legs were on the side nearest the hub (e.g., Fig. 4A–E). Many of the behavior patterns (both following and short-distance searching) were not absolutely constant, and the characterizations represent the most common types of movements rather than exhaustive lists of all movements. Some species were too small or moved too rapidly (especially *L. mariana*) for me to decipher the movements of certain legs in certain situations; lack of observations is indicated by “—”. Inconsistent behavior was also not characterized. Thus, for instance, some interior legs during sticky spiral construction only occasionally followed others, and were not counted as following. In sum, this table does not provide final characterizations of all leg movements, but rather illustrates two apparently general trends in the more consistent and easily observed types of leg movements: legs often follow the immediately anterior ipsilateral leg; and short distance searching movements by legs I and II tended to be prolateral in direction, while those by legs III and IV tended to be retrolateral. Family name abbreviations: AR – Araneidae; NE – Nephilidae; TET – Tetragnathidae; UL – Uloboridae.

Behavioral operation and spider	Following behavior (leading leg – following leg)	Not follow any leg	Direction of short-distance searching	
			Prolateral	Retrolateral
A. Secondary radius construction				
<i>Leucauge mariana</i> TET	I-II; II-I; I-I (contralateral) ^{1,2}	I; II	I; II	–
<i>Micrathena duodecimspinosa</i> AR	I-I ²	–	–	–
<i>Zosis geniculata</i> UL	oI-iI ²	–	–	–
B. Hub construction				
<i>L. mariana</i> TET	oI-oII; oII-oIII; oIII-oIV	oI; iIII ³	–	oIII ⁴ ; oIV ⁴
<i>M. duodecimspinosa</i> AR	oI-oII; oII-oIII; oIII-oIV	oI; iIII ³	oI; oII; iI; iII	oIII; oIV
<i>Z. geniculata</i> UL	oII-oIV; oIV-oIII ⁵	oIII; oII	–	–
C. Temporary spiral construction				
<i>L. mariana</i> TET	oII-oI; oIII-oII; oIV-oII ⁶	–	–	–
<i>Cyrtophora citricola</i> AR ⁷	oI-oII; oII-oIII	–	–	–
<i>Nephila clavipes</i> NE	oII-oIII; oIII-oIV; oI-oII ⁸	oI; oII; iI; iII; iIII	oI; oII; iI; iII	oIII; oIV
<i>Zosis geniculata</i> UL	oI-oII; oII-oIII; oIV-oII/oIII ⁹	iII; iIII ¹⁰	oI?; oII?	oIV
D. Sticky spiral construction				
<i>L. mariana</i> TET	oI-oII; oII-oIII; oIII-oIV ⁶	–	–	oIV(?)
<i>M. duodecimspinosa</i> AR	oII-oIII; oIII-oIV	oII	oI;oII	oIII?; oIV ¹¹
<i>Gasteracantha cauciformis</i> AR	oI-oII ¹² ; oII-oIII ¹³ ; oII/oIII-oIV ⁶	oII ¹¹	oI ¹⁴ ; oII ¹⁵	oII ¹⁴ ; oIV
<i>Araneus expletus</i> AR	oII-oIII; oIII-oIV; iI-iII; oI-iI	oII, iI	oI(?); oII(?); iI; iII	oIII; oIV
<i>Cyclosa monteverdii</i> AR	oII-oIII; oIII-oIV	iII; iIII	oII	oIII; oIV; iIII; iIV
<i>N. clavipes</i> NE	oIII-oIV ¹¹	oIII; oII; oI	–	oIII; oIV
<i>Zosis geniculata</i> UL	oI-oII ¹⁶ ; oII-oIII ¹³ ; oIII-oII ¹³ oI-iI ¹⁷ ; iI-oI ¹⁷ ; iIII-oIII ¹⁸	–	oI; oII ¹⁵	oIII ¹⁵

¹ all three following sequences were common; some other times these legs did not follow each other

² as legs I repeatedly grasped successive possible exit radii; in the *L. mariana* and *M. duodecimspinosa* there was no distinction between “inner” and “outer” leg I

³ During construction of the first loop the leg did not move at all

⁴ The movements were very rapid, so there is some uncertainty in this characterization.

⁵ oIV grasped r_n first, then oIII grasped it nearby. But oIV did not then immediately release its grip and move on; instead both legs held the radius as the sticky line was attached between them.

⁶ Leg oII often left the radius one or two frames of the video recording before oIV arrived; during this time oIII (which had followed oII) remained holding the same radius. The site grasped by oIV was closer to that grasped by oII than to that grasped by oIII. It is thus not entirely clear whether it should be said that oIV followed either oII or oIII.

⁷ construction of non-sticky spiral in dense horizontal sheet

⁸ Behavior occurred when spider interrupted temporary spiral construction to lay a tertiary radius

⁹ both oII and oIII were on r_n

¹⁰ at least following was not consistent

¹¹ the tarsus often appeared to slide (probably making contact on its retrolateral side) along r_n before gripping it

¹² oII followed oI to first seize r_n , but later did not follow oI during inner loop localization behavior when it occasionally grasped r_n briefly while it was tapping to locate the inner loop of sticky spiral

¹³ hand-over-hand movements reeling in or walking out r_n , with each leg grasping the radius outside the other; often only 1-2 steps.

¹⁴ when reached to grasp r_{n+1} , but not when tap to locate the inner loop

¹⁵ especially clear as oII and oIII pulled in or walked out r_n hand-over-hand

¹⁶ except on the first sticky spiral on r_n , when oI held the temporary spiral and oII grasped r_n .

¹⁷ infrequent

¹⁸ only the first step of leg oIII following an attachment

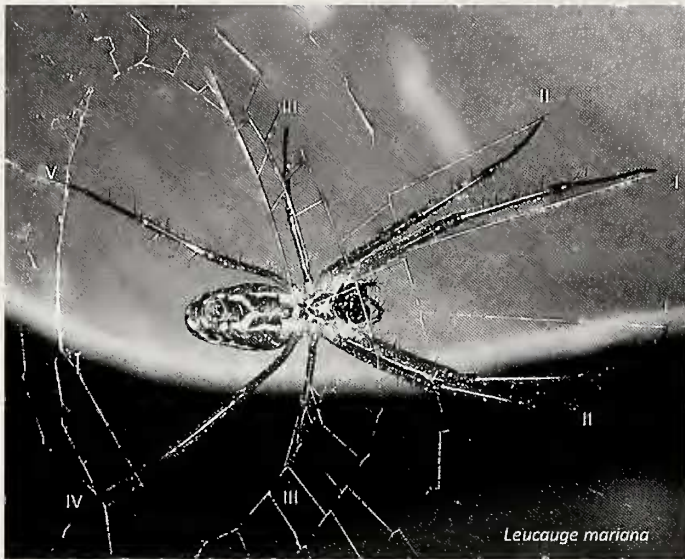


Figure 2.—A mature female *Leucauge mariana* in the typical resting posture at the hub. Legs I and II hold radii in the free zone, each of which is approximately parallel to the long axis of the leg.

indications regarding which side of the leg had made first contact.

The orientation of the tarsal claws with respect to the long axis of the leg while the tarsus grasped a line was checked under a dissecting microscope by observing the tarsi of mature females of the orb-weavers *Leucauge mariana*, *Argiope argentata* (Fabricius, 1775) (Araneidae), *Z. geniculata*, *N. clavipes*, and *Kukulcania hibernalis* (Hentz, 1842) (Filistatidae) that were resting immobile at the hub of an orb or other lines (in the case of *K. hibernalis*, in her retreat).

RESULTS

Following behavior.—Following behavior occurred during many stages of construction, including exploration and the construction of the radii, the hub, the temporary spiral, and the sticky spiral (Table 1). It was also taxonomically widespread, and occurred in all of the orb-weavers. Following behavior was sometimes facultatively omitted. For instance, *L. mariana* sometimes altered her usual “explore and then follow” behavior when she was in an area where the lines were so dense that her leg was likely to encounter a line nearby wherever she placed it. Facultative changes also occurred in some other contexts (Table 1). For instance, leg oIII followed leg iIII during sticky spiral construction in *Zosis geniculata* only in making its first step after the spider attached the sticky spiral to a radius.

Short-distance searching behavior.—The following leg often executed a small exploratory movement just before it contacted the line held by the leading leg; these movements probably functioned to locate the line, because the following leg never grasped exactly the same site that was being grasped by the leading leg. The short-distance searching movements made by following legs were asymmetrical in all species (Table 1). Legs I and II consistently moved prolaterally to find and grasp lines; legs III and IV, in contrast, moved retrolaterally. Neither the claws nor the accessory setae were visible in the

Possible ways to grasp lines that are parallel to long axis of the leg (hypotheses):

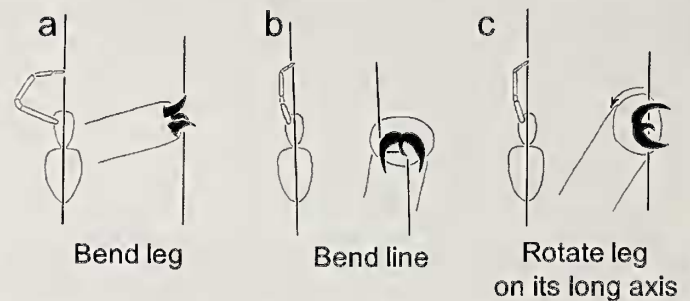


Figure 3.—Three theoretically possible ways in which a spider might orient her leg to grasp a line with her middle claw that was more or less parallel to the long axis of the leg: (a) bend the leg so that the long axis of the tarsus is perpendicular to the line; (b) bend the line so that it is perpendicular to the long axis of the leg at the point where the middle claw grasps it (Nielsen 1931); and (c) rotate the leg on its long axis so that the middle claw is perpendicular to the line.

video recordings, but the orientations of these movements presumably facilitated grasping the line with the asymmetrically placed middle claws and serrate accessory setae.

Grasping lines nearly parallel to the leg's long axis.—All species that were observed sometimes grasped lines that were more or less parallel to the longitudinal axis of the leg (Fig. 2). Three theoretically possible ways in which a spider might use the classic middle claw grasping mechanism to grasp such lines are illustrated in Fig. 3: bend the leg to orient the tarsus perpendicular to the line; bend the line itself (Nielsen 1931); and rotate the leg on its long axis. Bending the leg was ruled out by the leg positions observed: the long axis of the tarsus of the leg was often more or less parallel to the line (e.g., Fig. 2). Nielsen (1931) thought that, as often occurs with a human's grip on a rope, the line was bent where the tarsus seized it (“... any one pulling at a rope will quite naturally ... [bend] it just at the point where the hand is holding it...” p. 23). Observations under a dissecting microscope of tarsi I of *L. mariana* and *Z. geniculata*, and of tarsi IV of *Argiope argentata* and *N. clavipes* showed, however, that the line was not bent perceptibly in any of these species. Instead, in all four species, the tarsus was rotated on the long axis of the leg, bringing the middle claw into a position that was approximately perpendicular to the line, and thus allowing this claw to grasp the line (Fig. 4). In contrast, the tarsal claws of *K. hibernalis* made widely variable angles with the lines that they grasped, and the portion of the claw that touched the line also varied widely (Fig. 5); rotation, if it occurred, was not dramatic.

DISCUSSION

Following behavior.—The functional significance of following behavior seems clear: by reducing the need for her more posterior legs to wave and explore like a blind man's cane, the spider can move more quickly, and expend less energy. Some spiders, as might be expected, facultatively abandoned following behavior when the lines in the web were dense. The taxonomic distribution of following behavior has not

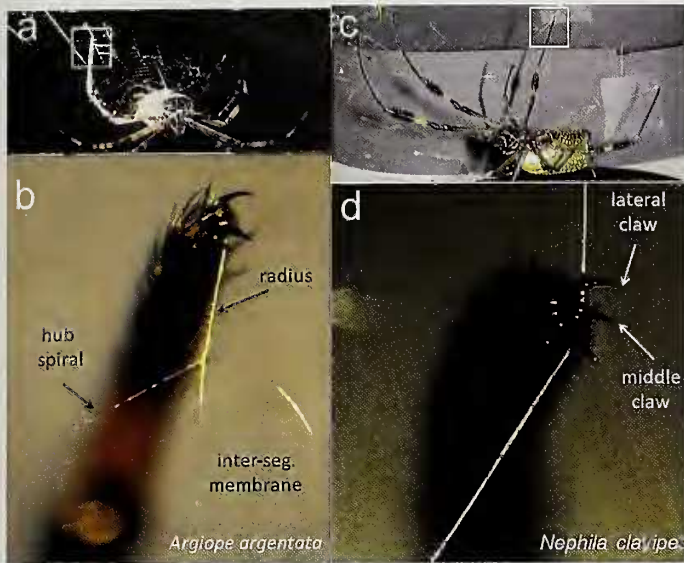


Figure 4.—Positions of *Argiope argentata* (a) and *Nephila clavipes* (c) as they rested on networks of lines, and closeup images of the tarsal claws of each (b and d respectively), as indicated by the rectangles in a and c. In both cases, the claws were rotated substantially on the long axis of the leg, and were approximately perpendicular to the line being grasped. Note the middle claw pressing on the line in d. In neither case is the line bent perceptibly to bring it perpendicular to the tarsus.

been determined. It appears to be widely used by orb-weavers (Table 1). To my knowledge, no survey of following in non-orb-weavers has ever been published. Following behavior was apparently absent in early instar nymphs of a ctenizid (likely *Ummidia*) that were filmed as they walked under lines to disperse (W. Eberhard, unpub.). But leg IV of the diplurid *Linothele macrothelifera* Strand, 1908 tended to follow ipsilateral leg III during sheet construction when the spider was walking on leaf litter and on the sheet of silk she had already laid (Eberhard & Hazzi 2013). Following may thus be an ancient trait, and may have already been present when early araneomorph spiders evolved to walk under aerial lines. Similar following behavior has evolved (presumably convergently) in the emesine bug *Stenolemus giraffe* (Hemiptera: Reduviidae: Emesinae), a predator of web spiders; posterior legs follow anterior legs as the bug walks in the webs of its prey (F. Soley, pers. comm.).

Asymmetrical short-distance searching behavior.—The tendency documented here for short-distance searches by legs I and II to be in a prolateral direction, and by legs III and IV in a retrolateral direction, complements the asymmetrical orientation of the middle claws and placement of the serrate accessory setae on these legs, and probably makes it easier for the leg to grasp the line when it makes contact. Presumably the evolution of the asymmetrical tarsal morphology was linked to the advantage of widening the area being searched by making laterally oriented searching movements.

One behavioral exception lends further support to the association between asymmetry in behavior and morphology. Inner loop localization behavior during sticky spiral construc-

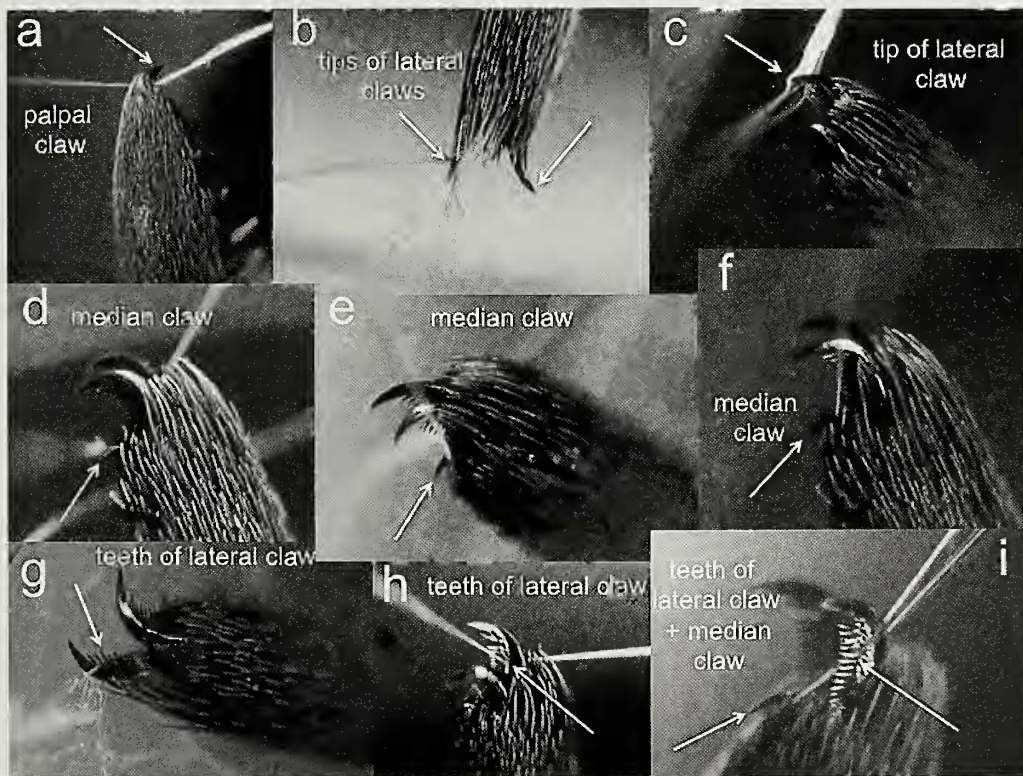


Figure 5.—Variations in the positions of tarsi and the lines that they held while a mature female *Kukulcania hibernalis* rested in her retreat. Lines were snagged by various structures in addition to the middle tarsal claw, and the orientations of lines with respect to the claws varied substantially.

tion involved legs movements to explore to encounter a line, but not to grasp it. Previous, naked eye observations suggested that legs tapped mostly in a dorso-ventral direction in this context (Eberhard 1982). The video recordings in this study confirmed that the movements of leg oI used to contact the inner loop were mainly dorso-ventral rather than lateral in the araneids *Araneus expletus* (O. P.-Cambridge, 1889), *Cyclosa monteverti*, *Gasteracantha cancriformis* (Linnaeus, 1758), and the uloborid *Zosis geniculata* (leg oI); a dorsally oriented, extension of oIV was employed in the nephilid *Nephila clavipes*. The tapping leg generally touched the inner loop only briefly (usually in only a single frame in the video recordings), and did not seize it.

Rotating legs to grasp lines.—The mechanism by which spiders rotated their legs to grasp lines that were approximately parallel to the leg's long axis is not certain, and will require further work. Two considerations suggest that the claws themselves did not rotate with respect to the tarsus. The three claws are solidly fused, and they have only two tendons attached to them, which are positioned to raise and lower the claws as a unit (Ramirez 2014). Secondly, changing the orientation of the middle claw without changing the positions of the serrate accessory setae against which the middle claw presses silk lines would not be advantageous for grasping lines. This suggests that the apparent rotation observed here occurred at an as yet undetermined more basal articulation. The tibia-patellar articulation is a potential site, as it has only a single condyle and four muscles, and might thus have relatively great mobility (Manton 1977; J. Runge, pers. comm.). Legs are known to rotate somewhat on their long axes when spiders walk upright on the substrate (J. Runge pers. comm.). Further observations will also be needed to determine the taxonomic extent of the ability to rotate legs on their long axes to grasp lines.

The coordination between rotation and other aspects of leg movement as the spider moves in her web also remains to be determined, and may be complex. It seems likely that the spider sometimes first senses the orientation of the line as she is first making contact with it, and then rotates her leg in the process of grasping the line. Such adjustments seem particularly likely to occur during long-distance searching behavior. An observation of *Z. geniculatus* under a dissecting microscope suggested, however, that rotation may sometimes occur earlier. When this spider moved one leg II to grasp a line that was already being held by her other leg II, the moving leg II was already rotated so that its middle claw was approximately perpendicular to this line. During following behavior, the leading leg might provide information on the orientation as well as the location of the line for the following leg. This could enable the spider to adjust the degree of rotation of her following leg before it contacted the line, facilitating its grasp of the line. These are, however, only conjectures at the moment.

Grasping lines in other contexts.—Spiders sometimes snag a line and then slide the tarsus along it smoothly; this is especially clear in species in which the dragline apparently slides through tarsal claw IV while the leg IV is extended posteriorly and is approximately parallel to the drag line. Presumably during sliding the leg is rotated and the middle claw is deflected ventrally only slightly, so that the line is

snagged on its ventral surface, but the claw is not strongly flexed ventrally and the serrated accessory setae are not bent sharply (Fig. 1) (Wilson 1962). I do not know the taxonomic distribution of this use of leg IV. It appears to be widely distributed in Orbicularia; in contrast, some mygalomorph and haplogynes such as filistatids (Eberhard 1986), and the entelegyne web building wolf spider *Aglaoctenus castaneus* (Mello-Leitão, 1942) (Lycosidae) (Eberhard & Hazzini in prep.) were not seen to slide the dragline through any claws (proving the absence of a behavior is difficult, however).

The ability to grasp lines firmly with leg IV probably enables the spider to lay lines under higher tensions than those needed to pull the lines from their spinnerets. Thus, the orb-weaver *Micrathena duodecimspinosa* (O. P.-Cambridge, 1890) (Araneidae) built frame and anchor lines under substantial tension; when she attached an anchor line to the substrate, she held the new line she was producing with one leg IV while she pulled herself forward on the substrate with her more anterior legs just prior to making the attachment (W. Eberhard, unpub.). The spider's movement onto the substrate just preceding an attachment of this sort was accompanied by increased tension on the dragline, as indicated by the angles formed with the web lines to which it was attached and also, in some cases, by displacement of the substrate itself (e.g., bending a flexible leaf). High tensions were particularly clear when the substrate to which the spider was attempting to attach was smooth: she scrabbled with her anterior legs, sometimes for many seconds, before getting a foothold and moving forward slightly and turning to make the attachment. In sum, the spider's ability to grasp her dragline firmly with leg IV allowed her to increase the tension on the line above that needed to pull silk from her spinnerets.

Limitations of this study.—For the orb-weavers of this study, the morphology of the middle claws and the serrated accessory setae, their positions on the tarsi, the following and short-distance searching behavior, rotation of the spider's legs, and the results of previous experimental manipulations of the setae (Foelix 1970), all argue strongly that the middle claws and the associated serrate accessory setae function in grasping silk lines. The distributions of serrate accessory setae and middle claws in other groups suggest, however, that this interpretation is incomplete.

Serrate accessory setae are probably ancient; the accessory setae of the austrochilids in the genera *Thaïda* Karsch, 1880 (Ramirez 2014), *Austrochilus* Gertsch & Zapfe, 1955 and *Hickmania* Gertsch, 1958 (Griswold et al. 2005) are similar in form and asymmetry to those of araneids such as *Araneus diadematus*. I have not made a comprehensive review, but perusal of two recent compendia (Griswold et al. 2005; Ramirez 2014) revealed several unexpected combinations of traits. Perhaps the greatest surprise is the senoculid *Senoculus* sp., which has both a middle claw and serrate accessory setae, with both displaced prolaterally on leg I (Ramirez 2014), just like the orb-weavers in the present study; but these are wandering spiders that apparently never make webs (Coville & Griswold 1983) (perhaps the tarsal modifications are used in climbing vertical draglines). Another puzzling combination of traits occurs in the web-building family Psecridae, which have 3 claws and walk under lines in their webs (Bristowe 1930; Eberhard 1987b; Zschokke & Vollrath 1995), but have

claw tufts rather than accessory setae (Griswold et al. 2005). Some spiders have a middle claw but lack serrate accessory setae (Griswold et al. 2005), and hang below lines when they are in their webs: these include Hypochilidae (Shear 1970; Eberhard 1988), Neolanidae (Griswold et al. 2005), Eresidae (e.g., Eberhard 1987b), and Psechridae (Eberhard 1987b; Zschokke & Vollrath 1995). The two compendia also document families in which spiders do not normally hang below their web lines and have tarsi with middle claws but that lack serrate accessory setae, including Amaurobiidae (Bristowe 1958), Oecobiidae (Glatz 1967), Cycloctenidae (Forster & Forster 1973), Desidae (Griswold et al. 2005), Huttonidae (Forster & Forster 1973), Segestriidae (Griswold et al. 2005), and Filistatidae (Griswold et al. 2005) (although a mature female of the filistatid *Kukulcania hibernalis*, which normally walks upright on its web or the substrate over which its web is stretched, chased a prey under a dense sheet of lines in an old web, and then walked hanging from the underside of this sheet with no apparent difficulty).

Nor are the middle claws of web spiders necessarily used to grasp lines. The tarsi of a *K. hibernalis* resting in her retreat illustrated a possible early stage in the evolution of the ability to grasp silk lines: angles between tarsal claws and lines varied widely, as did the portions of the claws which contacted the lines (Fig. 5). In all cases, the lines appeared to be only snagged, rather than grasped. The middle claws of this group may have different functions, such as bracing or hooking against the substrate as the spider moves. Perhaps some serrate setae and middle claws serve to allow the spider to climb vertical lines (though they are certainly not necessary to perform this behavior—see Eberhard 1986). There are still further subtleties in the middle claws of web builders, such as the concave surfaces on the retrolateral sides of the teeth of the middle claw (Nielsen 1931, M. J. Ramírez pers. comm.), whose functional significance is unclear.

In short, there are several mysteries yet to be unraveled regarding how spiders grasp and walk on lines. These remaining mysteries were graphically illustrated by the observation of a young unidentified sparassid, a group which has only two claws and a dense claw tuft rather than serrated accessory setae, literally sprinting up its dragline after being dislodged from its retreat (W. Eberhard, unpub.).

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LITERATURE CITED

- Barth, F.G. 2002. *A Spider's World Senses and Behavior*. Springer Verlag, New York.
- Bristowe, W.S. 1930. Notes on the biology of spiders. I. The evolution of spiders' snares. *Annals & Magazine of Natural History* 6:334–342.
- Bristowe, W.S. 1958. *The World of Spiders*. Collins, London.
- Coville, R.E. & C. Griswold. 1983. Nesting biology of *Trypoxylon xanthandrum* in Costa Rica with observations on its spider prey (Hymenoptera: Sphecidae; Araneae: Senoelidae). *Journal of the Kansas Entomological Society* 56:205–216.
- Eberhard, W.G. 1972. The web of *Uloborus diversus* (Araneae: Uloboridae). *Journal of Zoology* 166:417–465.
- Eberhard, W.G. 1981. Construction behaviour and the distribution of tensions in orb webs. *Bulletin of the British Arachnological Society* 5:189–204.
- Eberhard, W.G. 1982. Behavioral characters for the higher classification of orb-weaving spiders. *Evolution* 36:1067–1095.
- Eberhard, W.G. 1986. Trail line manipulation as a character for higher level spider taxonomy. Pp. 49–51. *In* Proceedings of the Ninth International Congress of Arachnology, Panamá 1983. (W. G. Eberhard, Y. D. Lubin, B. Robinson, eds.). Smithsonian Institution Press, Washington, DC.
- Eberhard, W.G. 1987a. Hub construction by *Leucage mariana* (Araneae, Araneidae). *Bulletin of the British Arachnological Society* 7:128–132.
- Eberhard, W.G. 1987b. Construction behavior of non-orb weaving cribellate spiders and the evolutionary origin of orb webs. *Bulletin of the British Arachnological Society* 7:175–178.
- Eberhard, W.G. 1988. Combing and sticky silk attachment behaviour by cribellate spiders and its taxonomic implications. *Bulletin of the British Arachnological Society* 7:247–251.
- Eberhard, W.G. & N. Hazzi. 2013. Web construction of *Linothele macrothelifera* (Araneae, Dipluridae). *Journal of Arachnology* 41:70–75.
- Eberhard, W.G. & N. Hazzi. 2017. Webs and building behavior of *Aglaoctenus castaneus* (Araneae: Lycosidae: Sosippinae). *Journal of Arachnology* 45: 177–197.
- Foelix, R. 1970. Structure and function of tarsal sensilla in the spider *Araneus diadematus*. *Journal of Experimental Zoology* 175:99–124.
- Foelix, R. 2011. *Biology of Spiders*. 3rd ed. Oxford University Press, New York.
- Forster, R.R. & L.M. Forster. 1973. *New Zealand Spiders: An Introduction*. Collins, London.
- Glatz, L. 1967. Zur Biologie und Morphologie von *Oecobius annulipes* Lucas (Araneae, Oecobiidae). *Zeitschrift für Morphologie der Tiere* 61:185–214.
- Griswold, C.E., M.J. Ramírez & J.A. Coddington. 2005. Atlas of phylogenetic data for entelegyne spiders (Araneae: Araneomorphae: Entelegynae) with comments on their phylogeny. *Proceedings of the California Academy of Sciences* 56:1–324.
- Hingston, R.W.G. 1922. The snare of the giant wood spider (*Nephila maculata*). Part II. The continuation of the snare. *Journal of the Bombay Natural History Society* 28:911–917.
- Manton, S.M. 1977. *The Arthropoda. Habits, Functional Morphology, and Evolution*. Clarendon Press, Oxford.
- Nielsen, E. 1931. *The Biology of Spiders*. Vols. I and II. Levin & Munksgaard, Copenhagen.
- Ramírez, M. 2014. The morphology and phylogeny of dionyehar spiders (Araneae: Araneomorphae). *Bulletin of the American Museum of Natural History* 390:1–374.
- Shear, W.A. 1970. Observations on the predatory behavior of the spider *Hypochilus gertschi* Hoffman (Hypochilidae). *Psyche* 76:407–417.
- Vollrath, F. 1992. Analysis and interpretation of orb spider exploration and web-building behavior. *Advances in the Study of Behavior* 21:147–199.
- Wilson, R.S. 1962. The control of dragline spinning in the garden spider. *Quarterly Journal of Microscopical Science* 104:557–571.
- Zschokke, S. & F. Vollrath. 1995. Web construction patterns in a range of orb-weaving spiders (Araneae). *European Journal of Entomology* 92:523–541.

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